ZooKeys 1278: 265–285 (2026)
DOI: 10.3897/zookeys.1278.189788

Research Article

Revision of the *Drabescus ineffectus* species group with descriptions of five new species from southern China (Hemiptera, Cicadellidae, Deltocephalinae)

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Abstract

Five new species of the leafhopper genus *Drabescus* (Hemiptera, Cicadellidae, Deltocephalinae) from southern China are described and illustrated: *Drabescus denticulatus* Qu, Li, Dietrich & Dai, *D. digitulatus* Qu, Li, Dietrich & Dai, *D. guangdongensis* Qu, Li, Dietrich & Dai, *D. millesimus* Li, Qu & Dai, and *D. trigonius* Qu, Li, Dietrich & Dai. These species are morphologically similar to *Drabescus ineffectus* (Walker, 1858) but can be distinguished by diagnostic differences in the male genitalia, particularly in the shape of the aedeagal shaft, processes, and associated structures. The *D. ineffectus* species group is established to accommodate these five new species and four other related species. Detailed descriptions, diagnoses, and illustrations are provided for all new taxa. An updated checklist and an identification key to males of the 41 known Chinese *Drabescus* species are also presented. Type specimens are deposited in the Institute of Entomology, Guizhou University (GUGC).

Key words: Morphology, new taxa, taxonomy

OPEN ACCESS

Academic editor:
J. Adilson Pinedo-Escatel
Received: 26 February 2026
Accepted: 26 March 2026
Published: 30 April 2026

ZooBank: https://zoobank.org/5F79A87C-1030-4E0F-AD6F-7A0C28D625D6

Citation: Qu L, Li Z, Dietrich CH, Li H, Jiang W, Dai R (2026) Revision of the *Drabescus ineffectus* species group with descriptions of five new species from southern China (Hemiptera, Cicadellidae, Deltocephalinae). ZooKeys 1278: 265–285. https://doi.org/10.3897/zookeys.1278.189788

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Introduction

The leafhopper genus *Drabescus* Stål, 1870 (Hemiptera, Cicadellidae, Deltocephalinae) (Zhang and Webb 1996; Lu et al. 2019) currently comprises 68 recognized species worldwide. China represents the centre of diversity for the genus, with 36 species recorded to date (Viraktamath et al. 2022; Xu and Zhang 2023). Recent taxonomic investigations have considerably expanded the known diversity of *Drabescus* in China, with several new species described in the past decade (Wang et al. 2016; Lu et al. 2019; Yu et al. 2019; Xu and Zhang 2023).

Recent field surveys in mountainous areas of Fujian, Guangdong, and Guangxi provinces, China, revealed five additional new species of *Drabescus*. These taxa closely resemble *D. ineffectus* in external morphology, sharing a yellowish-brown colouration with dark spots, a broad crown with a transverse anterior carina, and a transversely rugose pronotum. They also share the following combination of male genital characteristics: (1) aedeagus lacking basal

processes and curved dorsad in lateral view; (2) pygofer side with large, recurved posteroventral process; (3) connective Y-shaped in ventral view; (4) style long and slender. Despite these shared features, each species possesses diagnostic differences in male genital structures, particularly the structure of the aedeagus and pygofer process, allowing for reliable species delimitation. Based on the morphological similarity of the new species to *D. ineffectus*, we recognize a *D. ineffectus* species group to include the five new species described below, along with four previously known congeners: *D. bilaminatus* Yu, Webb, Dai & Yang, 2019, *D. henanensis* Zhang, Zhang & Chen, 1997, *D. ineffectus* (Walker, 1858), and *D. multipunctatus* Yu, Webb, Dai & Yang, 2019.

This study provides detailed morphological descriptions, diagnostic comparisons, and illustrations of the five new species. The taxonomic conclusions are based on detailed examination of male genital characters, which have been shown to be the most reliable features for species-level identification in *Drabescus* (Zhang and Webb 1996; Lu et al. 2019; Yu et al. 2019). Additionally, an updated checklist of the Chinese *Drabescus* species is provided.

Materials and methods

The specimens examined in this study were collected using sweep nets and light traps from Fujian Province (Guobao Township, Huboliao National Nature Reserve), Guangdong Province (Chebaling National Nature Reserve), and Guangxi Province (Huaping, Damingshan National Nature Reserves). Specimens were preserved either dry on triangular cards or in ethanol. All holotypes, paratypes and other specimens examined are deposited in the Institute of Entomology, Guizhou University (**GUGC**).

Morphological observations and measurements were carried out using a Keyence VHX-1000 digital microscope. Body dimensions were measured as follows: total length from the vertex apex to the tip of the folded forewings; head width at the widest point across the eyes; and pronotum width at its maximum. All measurements are given in millimetres and follow the protocol of Zhang and Webb (1996).

For the examination of male genitalia, the abdomen was removed and cleared in 10% NaOH solution heated at 100 °C for 1–3 min. The treated tissue was rinsed in distilled water and dissected in glycerine. The extracted genital structures were preserved in micro-vials filled with glycerine, which were pinned beneath the source specimen. Illustrations were made with the aid of a camera lucida attached to an Olympus SZX7 stereomicroscope. Final figures were prepared and arranged using Adobe Illustrator CS6.

Taxonomy

Drabescus Stål

Drabescus Stål, 1870: 738; Zhang and Webb 1996: 23. Type species: *Bythoscopus remotus* Walker, 1851.

Paradrabescus Kuoh, 1985: 379? Type species: *Paradrabescus testaceus* Kuoh, 1985.

Drabescus (*Ochrescus*) Anufriev & Emeljanov, 1988: 174. Type species: *Drabescus ochrifrons* Vilbaste, 1988.

Drabescus (*Leucostigmidium*) Anufriev & Emeljanov, 1988: 174. Type species: *Drabescus nigrifemoratus* Matsumura, 1971.
Tylissus Stål, 1870: 739. Type species: *Tylissus nitens* Stål, 1870.

Checklist of *Drabescus* species in China

***D. albofasciatus* Cai & He, 1998**
D. albofasciatus Cai & He, 1998: 24, fig. 5; Lu et al. 2019: 240–241, fig. 1.
Distribution: China (Henan).

***D. albosignus* Li & Wang, 2005**
D. albosignus Li & Wang, 2005: 175–176, fig. 6.
Distribution: China (Guizhou, Henan).

***D. albostriatus* Yang, 1995**
D. albostriatus Yang, 1995: 42–43, fig. 7.
Distribution: China (Zhejiang).

***D. atratus* Kato, 1933**
D. atratus Kato, 1933: 456, pl. 14, fig. 17.
Distribution: China (Taiwan), Japan.

***D. bilaminatus* Yu, Webb, Dai & Yang, 2019**
D. bilaminatus Yu et al., 2019: 45, figs 1–9.
Distribution: China (Guangxi).

***D. convolutus* Wang, Qu, Xing & Dai, 2016**
D. convolutus Wang et al., 2016: 122, figs 32, 33, 42–47.
Distribution: China (Guizhou).

***D. cuspidatus* Wang, Qu, Xing & Dai, 2016**
D. cuspidatus Wang et al., 2016: 120, figs 30, 31, 36–41.
Distribution: China (Hainan, Guangxi).

***D. denticulatus* Qu, Li, Dietrich & Dai, sp. nov.**
Distribution: China (Fujian).

***D. digitulatus* Qu, Li, Dietrich & Dai, sp. nov.**
Distribution: China (Fujian).

***D. extensus* Kuoh, 1985**
D. extensus Kuoh, 1985: 377–378, figs 1, 2; Zhang and Webb 1996: 24, fig. 515.
Distribution: China (Yunnan).

***D. formosanus* Matsumura, 1912**
D. formosanus Matsumura, 1912: 294–295; Zhang and Webb 1996: 24, figs 375–379, 540.
D. trichromus Yang, 1995: 41–42, fig. 6. Synonymized by Zhang and Webb 1996: 24.
Distribution: China (Taiwan, Zhejiang, Guangdong, Fujian, Guizhou).

***D. furcatus* Cai & Jiang, 2002**
D. furcatus Cai & Jiang, 2002: 16–17, figs 1–8.
Distribution: China (Henan, Hubei).

***D. fuscorufous* Kuoh, 1985**
D. fuscorufous Kuoh, 1985: 378, figs 3, 4; Zhang and Webb 1996: 24, fig. 518.
Distribution: China (Yunnan).

***D. gracilis* Li & Wang, 2005**
D. gracilis Li & Wang, 2005: 174–175, fig. 5.
Distribution: China (Guizhou).

***D. guangdongensis* Qu, Li, Dietrich & Dai, sp. nov.**
Distribution: China (Guangdong).

***D. hainanensis* Lu, Webb & Zhang, 2019**
D. hainanensis Lu et al., 2019: 242–244, fig. 2.
Distribution: China (Hainan).

***D. henanensis* Zhang, Zhang & Chen, 1997**
D. henanensis Zhang et al., 1997: 239–240, fig. 3.
Distribution: China (Henan).

***D. ineffectus* (Walker, 1858)**
Bythoscopus ineffectus Walker, 1858: 266.
D. ineffectus (Walker, 1858)—Distant 1908a: 145; Zhang and Webb 1996: 24, figs 72, 320–326, 541.
Distribution: China (Guangxi, Hubei, Henan, Anhui), Russia, Japan, Korea, Lithuania.

***D. jinxiuensis* Zhang & Shang, 2003**
D. jinxiuensis Zhang & Shang, 2003: 96–97, fig. 1.
Distribution: China (Guangxi).

***D. lamellatus* Zhang & Shang, 2003**
D. lamellatus Zhang & Shang, 2003: 99–100, fig. 3.
Distribution: China (Gansu, Guangxi).

***D. lii* Zhang & Shang, 2003**
D. lii Zhang & Shang, 2003: 97–99, fig. 2.
Distribution: China (Guizhou, Hubei).

***D. limbaticeps* (Stål, 1858)**
Selenocephalus limbaticeps Stål, 1858: 453.
D. limbaticeps (Stål, 1858)—Melichar 1903: 170–171; Viraktamath et al. 2022: 236–237, figs 1K, L, 2I, 3F, 4F, G, 5C, 9A–G.
D. conspicuus Distant, 1908b: 306, fig. 195; Kuoh 1966: 118, fig. 106. Synonymized by Zhang and Webb 1996: 24, figs 358–362, 530.
Distribution: China (Guizhou, Yunnan, Taiwan), India, Japan, Philippines, Sri Lanka.

***D. macrocladus* Xu & Zhang, 2023**
D. macrocladus Xu & Zhang, 2023: 394–404, figs 1, 2.
Distribution: China (Hainan).

***D. minipenis* Zhang, Zhang & Chen, 1997**
D. minipenis Zhang et al., 1997: 240–241, fig. 4.
Distribution: China (Henan, Shanxi, Shaanxi, Yunnan, Hubei, Taiwan).

***D. mucronatus* Xu & Zhang, 2023**
D. mucronatus Xu & Zhang, 2023: 394–404, figs 3, 4.
Distribution: China (Guangdong, Hunan).

***D. multidentatus* Wang, Qu, Xing & Dai, 2016**
D. multidentatus Wang et al., 2016: 123–124, figs 34, 35, 48–53.
Distribution: China (Shanxi).

***D. multipunctatus* Yu, Webb, Dai & Yang, 2019**
D. multipunctatus Yu et al., 2019: 45–48, figs 10–18.
Distribution: China (Hainan).

***D. nervosopunctatus* Signoret, 1880**
D. nervosopunctatus Signoret, 1880: 209, pl. 7, fig. 72; Kuoh 1966: 117–118, fig. 105; Zhang and Webb 1996; 25, figs 413–417, 527; Viraktamath et al. 2022: 237–238, figs 2A, B, J, 3G, 5E, 10A–H.
Distribution: China (Guizhou, Jiangxi, Yunnan, Hubei, Taiwan), India, Indonesia.

***D. nitobei* Matsumura, 1912**
D. nitobei Matsumura, 1912: 290–291; Zhang and Webb 1996: 25, figs 345–349, 538; Shang and Zhang 2007: 430–431, fig. 1.
Distribution: China (Hainan, Guangxi, Hebei, Taiwan), Japan, Russia, India.

***D. notatus* Schumacher, 1915**
D. notatus Schumacher, 1915: 99; Zhang and Webb 1996: 25.
Distribution: China (Taiwan).

***D. ogumae* Matsumura, 1912**
D. ogumae Matsumura, 1912: 291–292; Kuoh 1966: 116–117, fig. 104; Zhang and Webb 1996: 25, pl. 1, figs 418–424.
Distribution: China (Guizhou, Jiangxi, Guangdong, Yunnan, Shanxi, Shandong, Taiwan), Japan.

***D. pallidus* Matsumura, 1912**
D. pallidus Matsumura, 1912: 293; Zhang and Webb 1996: 25, pl. 1, figs 351–357.
Distribution: China (Shaanxi, Shanxi, Hubei), Japan, North Korea.

***D. pellucidus* Cai & Shen, 1999**
D. pellucidus Cai & Shen, 1999: 28–29, fig. 5.
Distribution: China (Henan, Hubei).

***D. piceatus* Kuoh, 1985**

D. piceatus Kuoh, 1985: 378–379, figs 5–8; Zhang and Webb 1996: 25, figs 425–430, 529; Zhang et al. 1997: 241–242, fig. 5.

Distribution: China (Yunnan, Henan, Hubei).

***D. piceus* (Kuoh, 1985)**

Paradrabescus piceus Kuoh, 1985: 381, figs 16–19.

D. piceus (Kuoh, 1985)—Zhang and Webb 1996: 25, fig. 521.

Distribution: China (Yunnan).

***D. quadrispinosus* Shang, Webb & Zhang, 2014**

D. quadrispinosus Shang et al., 2014: 143, fig. 1.

Distribution: China (Sichuan, Gansu).

***D. shillongensis* Rao, 1989**

D. shillongensis Rao, 1989: 65; Zhang and Webb 1996: 25, figs 392–396, 532; Shang and Zhang 2007: 431–432, fig. 2; Viraktamath et al. 2022: 239–246, figs 2E, F, L, 3I, 5G, 12A–H.

Distribution: China (Guizhou, Guangdong, Yunnan), India, Vietnam.

***D. millesimus* Li, Qu & Dai, sp. nov.**

Distribution: China (Guangxi).

***D. testaceus* (Kuoh, 1985)**

Paradrabescus testaceus Kuoh, 1985: 380–381, figs 9–15.

D. testaceus (Kuoh, 1985)—Zhang and Webb 1996: 25, figs 397–402, 533.

Distribution: China (Hubei, Yunnan), Thailand.

***D. trigonius* Qu, Li, Dietrich & Dai, sp. nov.**

Distribution: China (Guangxi).

***D. vilbastei* Zhang & Webb, 1996**

D. vilbastei Zhang & Webb, 1996: 26, figs 339–343, 528.

Distribution: China (Anhui, Henan, Guizhou, Shaanxi, Shanxi), Japan, Russia.

Key to males of the Chinese species of *Drabescus*

Note: Excluded species (known only from females or of undetermined sex): *D. albostriatus*, *D. atratus*, *D. extensus*, *D. fuscorufous*, *D. notatus*, *D. piceus*.

1 Head triangularly produced in dorsal view; median length about three times length next to eye (Xu and Zhang 2023: fig. 3) ..... ***D. mucronatus***

– Head rounded or angularly produced in dorsal view; median length sub-equal to, or less than twice, length next to eye..... **2**

2 Head with anterior margin broadly rounded in lateral view (Lu et al. 2019: fig. 2B) ..... ***D. hainanensis***

– Head with anterior margin distinctly angulate in lateral view..... **3**

3 Pygofer side without process, apex rounded **4**

– Pygofer side with a process or apex acute..... **12**

4 Basal processes of aedeagal shaft bifurcate apically **5**
– Basal processes of aedeagal shaft not bifurcate **9**
5 Aedeagal basal processes with multiple apical branches (Shang and Zhang 2003: fig. 1F, G) ..... ***D. jinxiuensis***
– Aedeagal basal processes with single apical branch **6**
6 Aedeagal shaft subapically inflated in ventral view **7**
– Aedeagal shaft not subapically inflated in ventral view **8**
7 Valve triangular; subgenital plate extremely slender; aedeagus weakly subapically inflated (Cai and Jiang 2002: figs 1–8) ..... ***D. furcatus***
– Valve semicircular; subgenital plate robust; aedeagus strongly subapically inflated (Shang and Zhang 2003: fig. 3) ..... ***D. lamellatus***
8 Head width at middle less than interocular width; subgenital plates almost straight (Shang and Zhang 2003: fig. 2A, C) ..... ***D. lii***
– Head width at middle greater than interocular width; subgenital plates slightly curved (Li and Wang 2005: fig. 5) ..... ***D. gracilis***
9 Connective Y-shaped, stem long **10**
– Connective U-shaped, stem short (Cai and Shen 1999: fig. 5) ... ***D. pellucidus***
10 Aedeagal basal processes shorter than shaft **11**
– Aedeagal basal processes longer than shaft (Xu and Zhang 2023: fig. 2M) ..... ***D. macrocladus***
11 Aedeagal processes dorsally curved with smooth margins in lateral view (Zhang and Webb 1996: fig. 429) ..... ***D. piceatus***
– Aedeagal processes straight with crenulate margins in lateral view (Zhang et al. 1997: fig. 4) ..... ***D. minipenis***
12 Pygofer side processes serrate-edged **13**
– Pygofer side apex acute or with single smooth process **23**
13 Aedeagal shaft with a single pair of extremely long basal processes extending far beyond shaft apex (Zhang and Webb 1996: fig. 376) .... ***D. formosanus***
– Aedeagal shaft processes not as above **14**
14 Aedeagal shaft wider dorsoventrally than laterally **15**
– Aedeagal shaft wider laterally than dorsoventrally **19**
15 Aedeagal shaft not dorsally inflated at midlength in lateral view **16**
– Aedeagal shaft dorsally inflated at midlength in lateral view **18**
16 Aedeagal shaft with minute triangular processes in ventral view; ventral margin crenulate in lateral view (Fig. 6G, H) ..... ***D. millesimus* sp. nov.**
– Aedeagal shaft not as above **17**
17 Aedeagal shaft abruptly subapically constricted into a cylindrical extension toward apex in ventral view; subapical inflation in lateral view (Fig. 7H) ..... ***D. trigonius* sp. nov.**
– Aedeagal shaft gradually tapered in ventral view; subapically inflated in lateral view (Fig. 3G, H) ..... ***D. denticulatus* sp. nov.**
18 Aedeagal shaft inflated both dorsally and ventrally in lateral view (Fig. 4G, H) ..... ***D. digitulatus* sp. nov.**
– Aedeagal shaft only dorsally inflated in lateral view (Fig. 2N) ... ***D. henanensis***
19 Aedeagal shaft gradually tapering from base to apex in lateral view **20**
– Aedeagal shaft distinctly inflated at middle in lateral view **22**
20 Aedeagal shaft truncate apically; style with serrate inner margin (Fig. 2K, P) ..... ***D. multipunctatus***
– Aedeagal shaft rounded apically; style inner margin smooth (Fig. 2J) ... **21**

21 Aedeagal shaft with long basal processes (Shang et al. 2014: fig. 1) ..... ***D. quadrispinosus***
– Aedeagal shaft without basal processes (Fig. 2J) ..... ***D. ineffectus***
22 Aedeagal shaft subapically inflated; dorsal margin with small teeth in lateral view (Fig. 2E) ..... ***D. bilaminatus***
– Aedeagal shaft medially inflated; dorsal margin smooth (Fig. 5G, H) ..... ***D. guangdongensis* sp. nov.**
23 Aedeagus with processes **24**
– Aedeagus without processes (Wang et al. 2016: figs 39, 40) ..... ***D. cuspidatus***
24 Aedeagal shaft with more than one pair of processes **25**
– Aedeagal shaft with only one pair of processes **26**
25 Aedeagal shaft with lateral basal processes slightly shorter than shaft (Zhang and Webb 1996: fig. 341) ..... ***D. vilbastei***
– Aedeagal shaft with lateral basal processes about half length of shaft (Zhang and Webb 1996: fig. 357) ..... ***D. pallidus***
26 Length of basal processes of aedeagal shaft more than 3/4 aedeagal shaft length **27**
– Length of basal processes of aedeagal shaft less than 3/4 aedeagal shaft length **30**
27 Aedeagal shaft apically inflated in lateral view (Li and Wang 2005: fig. 6) ..... ***D. albosignus***
– Aedeagal shaft apically tapered in lateral view **28**
28 Aedeagus shaft laterally compressed; basal processes stout, apices remote from shaft (Zhang and Webb 1996: figs 414, 416) ..... ***D. nervosopunctatus***
– Aedeagus shaft cylindrical; basal processes slender, apices close to shaft **29**
29 Aedeagus with small triangular ventral processes; dorsal margin of basal process serrate (Wang et al. 2016: figs 51, 52) ..... ***D. multidentatus***
– Aedeagus lacking triangular process (Zhang and Webb 1996: figs 400, 402) ..... ***D. testaceus***
30 Pygofer side with ventral margin serrate; aedeagal processes flattened (Zhang and Webb 1996: figs 418, 424) ..... ***D. ogumae***
– Pygofer side and aedeagal processes not as above **31**
31 Aedeagal processes no more than 1/3 as long as shaft **32**
– Aedeagal processes more than half as long as shaft **33**
32 Aedeagal processes near base of shaft (Zhang and Webb 1996: figs 361, 362) ..... ***D. limbaticeps***
– Aedeagal processes at or distad of mid-length of shaft (Lu et al. 2019: fig. 1F) ..... ***D. albofasciatus***
33 Aedeagus shaft elongate, cylindrical, straight in lateral view (Zhang and Webb 1996: fig. 396) ..... ***D. shillongensis***
– Aedeagus shaft shorter, tapering apically and dorsally curved in lateral view **34**
34 Connective stem about twice as long as arms (Wang et al. 2016: fig. 47) ..... ***D. convolutus***
– Connective stem subequal in length to arms (Zhang and Webb 1996: fig. 346) ..... ***D. nitobei***

Definition of the *Drabescus ineffectus* species group

Figs 1, 2

The *D. ineffectus* species group is established here to accommodate a cluster of species that are morphologically similar to *D. ineffectus* and share a distinct suite of characters in the male genitalia. Members of this group can be recognized by the following combination of features.

Diagnosis. Overall colouration yellowish-brown. Medium-sized to large leafhoppers, body length 6–12 mm. Head short and broad, crown with transverse anterior carina; anterior margin rounded or weakly produced in dorsal view, nearly parallel to posterior margin. Ocelli located on marginal carina of crown, distant from eyes. Pronotum transversely rugose with dense fine punctures, lateral margin slightly longer than that of crown. Hind femur macrosetal formula 2+2+1.

Pygofer with several macrosetae distributed on apical portion, with single, large, recurved posteroventral process bearing smaller teeth or spines in some species. Valve usually semicircular. Subgenital plate subtriangular, broad at base and narrow at apex, lateral margin convex with minute setae. Style relatively slender and elongate, apex digitiform. Connective Y-shaped with stem as long as or longer than arms. Aedeagal shaft curved dorsad, without processes; gonopore apicoventral.

Remarks. The *D. ineffectus* species group is primarily distributed in southern China. The group can be distinguished by the pygofer with a single large, dorsally curved posteroventral; the relatively elongate style; the subgenital plates with broadly convex lateral margins; and the aedeagus lacking basal processes.

Species included of *Drabescus ineffectus* species group

D. bilaminatus Yu, Webb, Dai & Yang, 2019
D. denticulatus Qu, Li, Dietrich & Daii, sp. nov.
D. digitulatus Qu, Li, Dietrich & Dai, sp. nov.
D. guangdongensis Qu, Li, Dietrich & Dai, sp. nov.
D. henanensis Zhang, Zhang & Chen, 1997
D. ineffectus (Walker, 1858)
D. multipunctatus Yu, Webb, Dai & Yang, 2019
D. millesimus Li, Qu & Dai, sp. nov.
D. trigonius Qu, Li, Dietrich & Dai, sp. nov.

Drabescus denticulatus Qu, Li, Dietrich & Dai, sp. nov.

https://zoobank.org/2FC8F5C0-C422-411B-AE38-6E0A23247C0E

Fig. 3

Material examined. • ***Holotype***, ♂ (GUGC), CHINA: Fujian Province, Wuyishan National Forest Park, 23.V.2012, collected by Jiankun Long. • ***Paratype***, 1♂ (GUGC), same data as holotype.

Description. Length (including tegmen): 11.0–11.5 mm.

Body yellowish brown, densely covered with minute black spots and irregular patches; face uniformly bright yellow; forewing with hyaline patch near apex of clavus. Crown anterior margin broadly rounded and protruding with transverse striations. Ocelli each separated from adjacent eye by slightly more than three

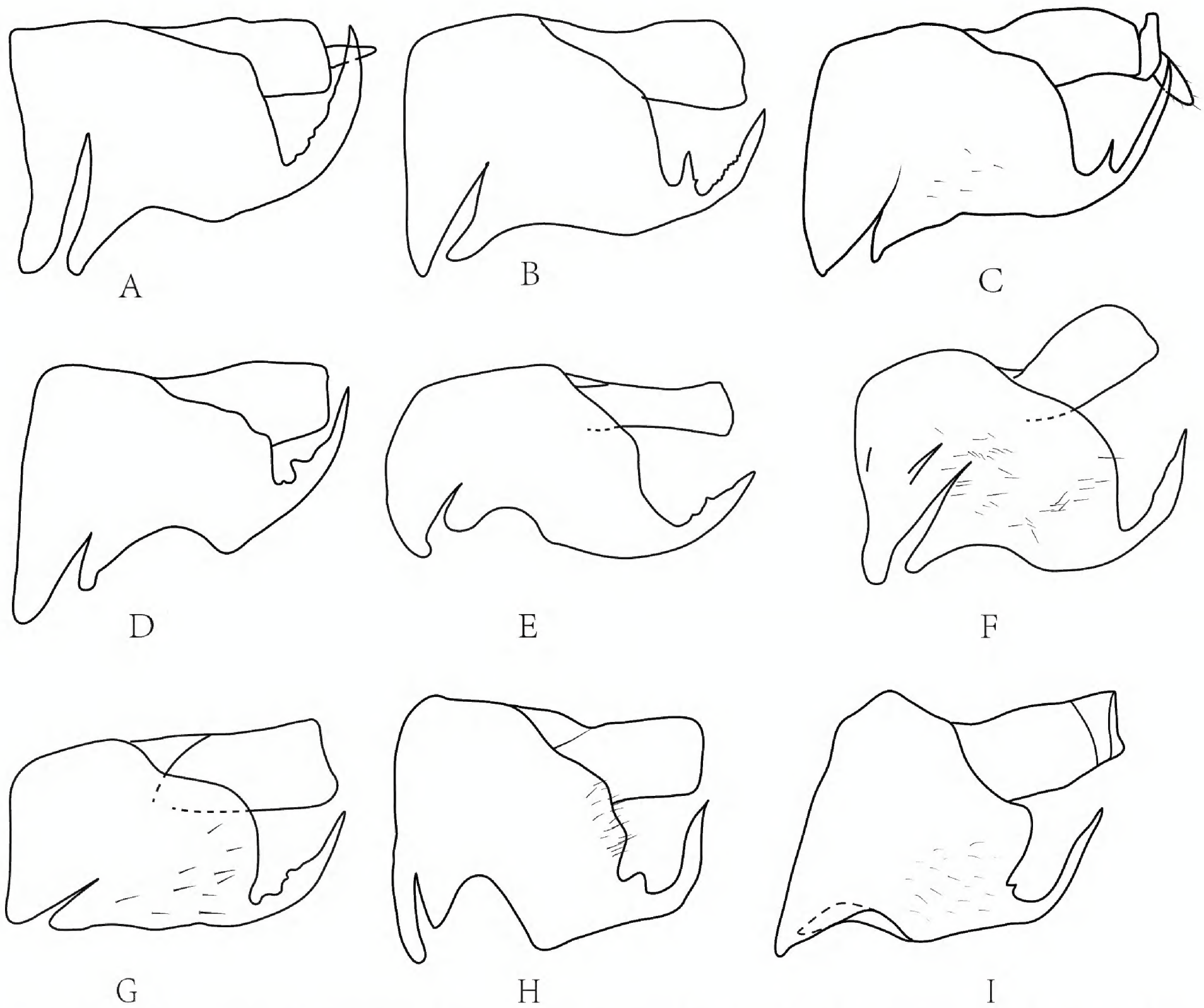

Figure 1. Pygofers of *Drabescus ineffectus* group species in lateral view. **A.** *D. bilaminatus* (after Yu et al. 2019); **B.** *D. denticulatus* sp. nov.; **C.** *D. digitulatus* sp. nov.; **D.** *D. guangdongensis* sp. nov.; **E.** *D. henanensis* (after Zhang et al. 1997); **F.** *D. ineffectus* (after Zhang and Webb 1996); **G.** *D. multipunctatus* (after Yu et al. 2019); **H.** *D. trigonius* sp. nov.; **I.** *D. millesimus* sp. nov.

ocellar diameters. Face, including eyes, distinctly broader than long. Frontoclypeus slightly expanded apically. Clypeal suture weakly defined; frontoclypeal sulcus sharply impressed.

***Male genitalia*.** Male pygofer side subquadrate, sparsely microsetose; posteroventral process long, curved dorsomedially with serrate inner edge and distinct dorsal spine near base. Valve triangular to semicircular. Subgenital plate with digitate apical extension relatively long. Style with apical portion smoothly rounded and curved mesad. Aedeagus shaft dorsoventrally flattened, margins undulate, lanceolate-arrowhead-shaped in ventral view, with lateral margins finely serrate near midlength; shaft inflated at midlength in lateral view; gonopore subapical on ventral surface. Connective stem and arms subequal in length.

Distribution. China (Fujian: Wuyishan).

Etymology. The new species name is a Latin adjective derived from *denticulus* (toothed), referring to the finely toothed (denticulate) margin of the aedeagus.

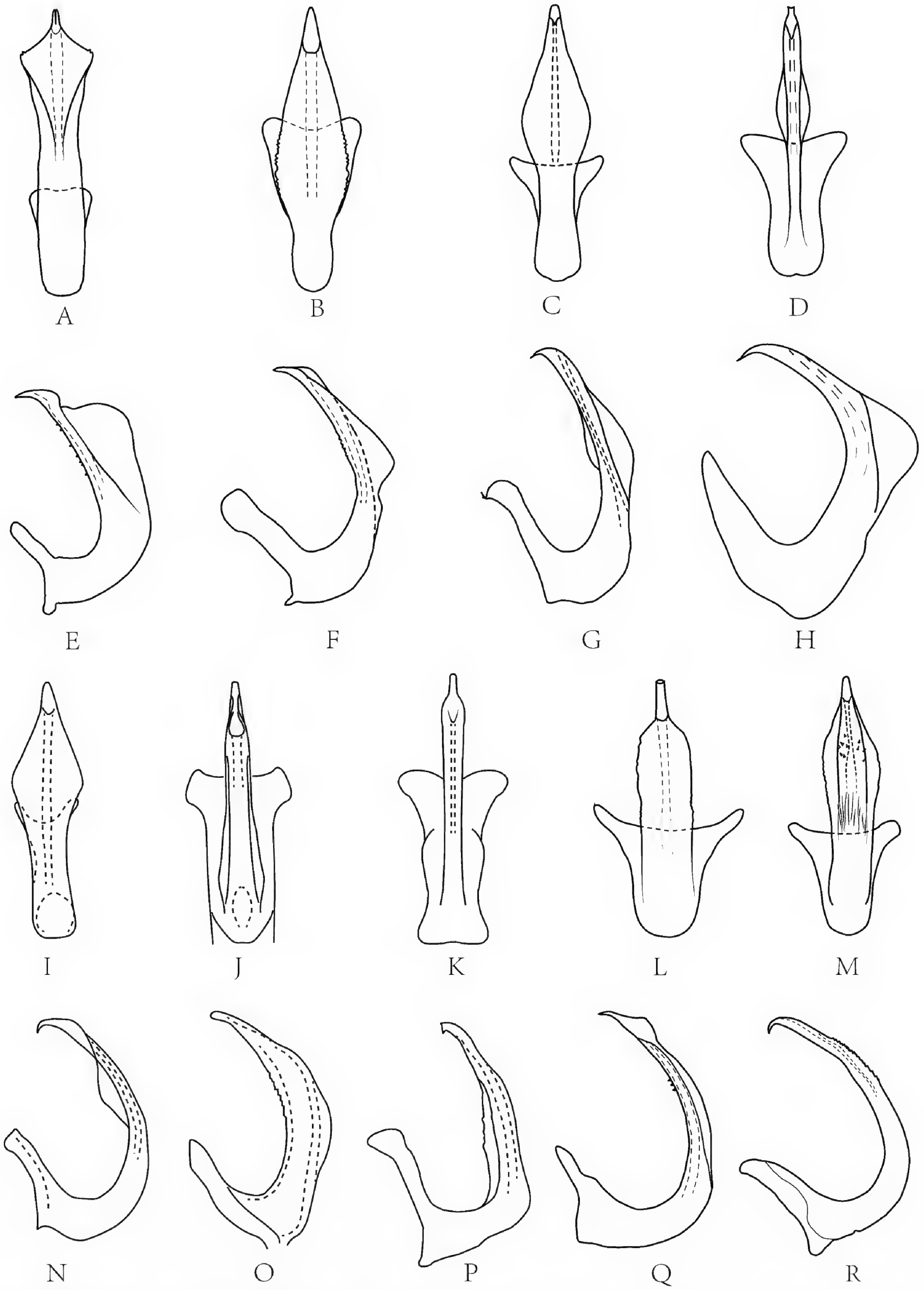

Figure 2. Aedeagus of *Drabescus ineffectus* group species in ventral (**A–D, I–M**) and lateral view (**E–H, N–R**). **A, E.** *D. bilaminatus* (after Yu et al. 2019); **B, F.** *D. denticulatus* sp. nov.; **C, G.** *D. digitulatus* sp. nov.; **D, H.** *D. guangdongensis* sp. nov.; **I, N.** *D. henanensis* (after Zhang et al. 1997); **J, O.** *D. ineffectus* (after Zhang and Webb 1996); **K, P.** *D. multipunctatus* (after Yu et al. 2019); **L, Q.** *D. trigonius* sp. nov.; **M, R.** *D. millesimus* sp. nov.

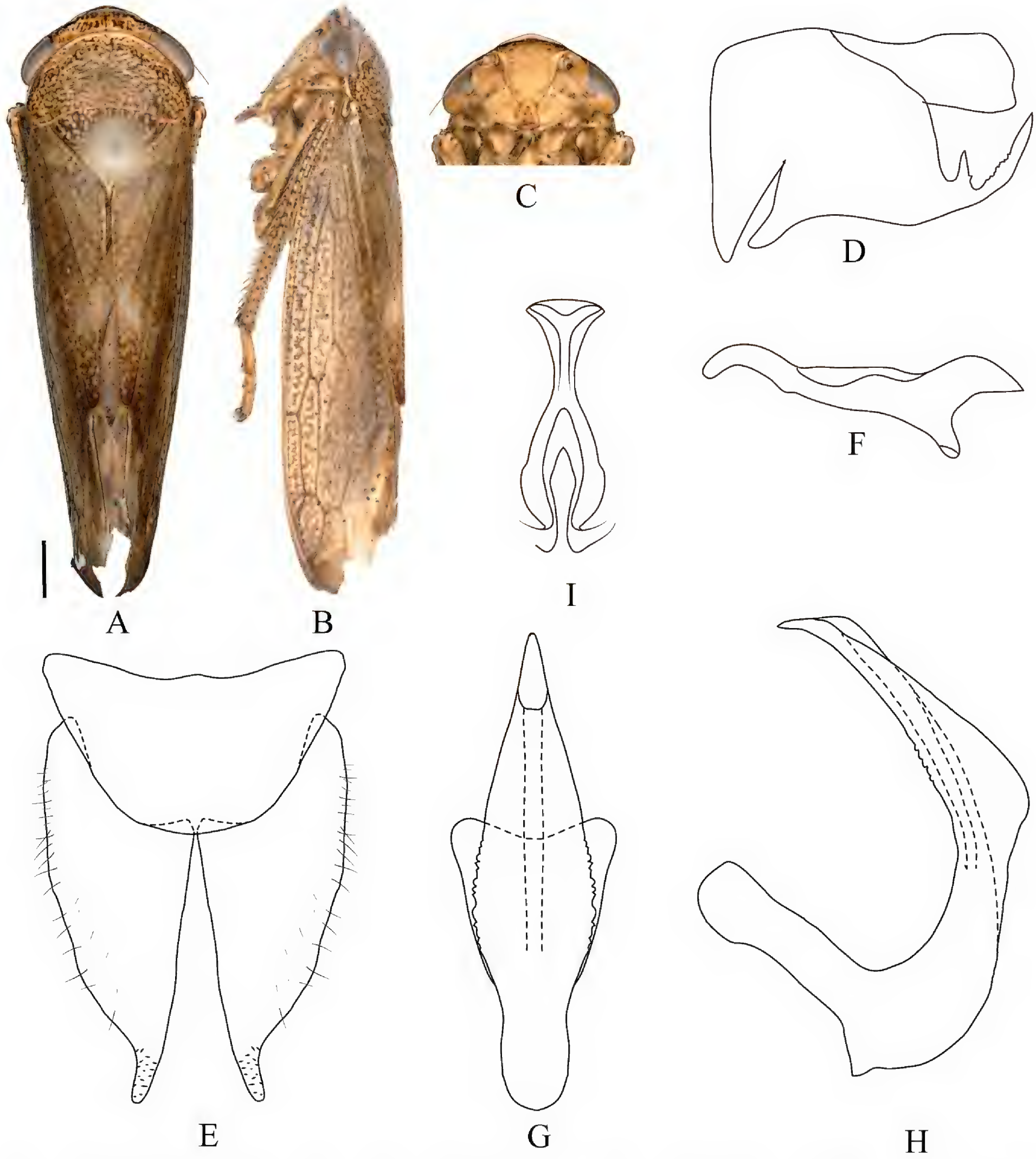

Figure 3. *Drabescus denticulatus* Qu, Li, Dietrich & Dai, sp. nov. **A.** Male habitus, dorsal view; **B.** Same, lateral view; **C.** Face; **D.** Pygofer, lateral view; **E.** Valve and subgenital plate, ventral view; **F.** Style, dorsal view; **G.** Aedeagus, ventral view; **H.** Same, lateral view; **I.** Connective, ventral view. Scale bars: 1.0 mm (**A–C**).

Remarks. The new species is externally indistinguishable from *D. ineffectus*, but the male genitalia exhibit the following diagnostic differences: aedeagal shaft gradually expanded from base to middle then tapered evenly toward apex (continuously narrowed from base to tip in *D. ineffectus*); in lateral view, shaft with two conspicuous swellings at mid-length and another subapically (shaft with single median inflation in *D. ineffectus*, subapical region unmodified); pygofer side with smaller dorsal spine at base of posteroventral process (without spine in *D. ineffectus*).

***Drabescus digitulatus* Qu, Li, Dietrich & Dai, sp. nov.**
https://zoobank.org/CAECB98A-E1CC-46BE-976D-3ECAD4C6793A
Fig. 4

Material examined. • ***Holotype***, ♂ (GUGC), CHINA: Fujian Province, Guobao Township, 11.V.2012, collected by Jiankun Long. • ***Paratypes***, 1♂ (GUGC), same locality as holotype; 1♂ (GUGC), CHINA: Fujian Province, Huboliao National Nature Reserve (light trap), 21.V.2013, collected by Meng Jiao and Bin Li.

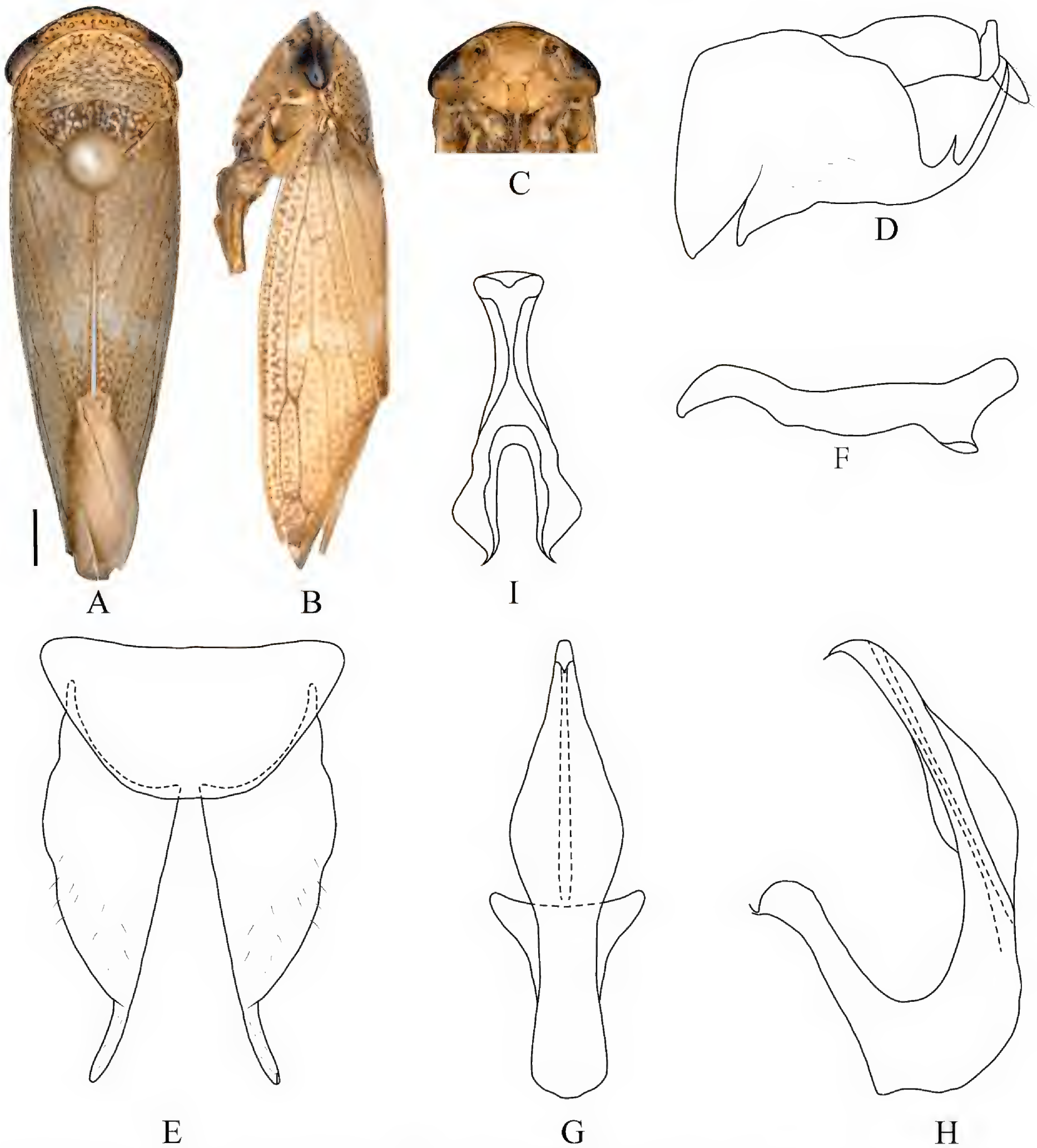

Figure 4. *Drabescus digitulatus* Qu, Li, Dietrich & Dai, sp. nov. **A.** Male habitus, dorsal view; **B.** Same, lateral view; **C.** Face; **D.** Pygofer, lateral view; **E.** Valve and subgenital plate, ventral view; **F.** Style, dorsal view; **G.** Aedeagus ventral view; **H.** Same, lateral view; **I.** Connective, ventral view. Scale bars: 1.0 mm (**A–C**).

Description. Length (including tegmen): 10.5–11.0 mm.

Body yellowish brown; crown, pronotum, and scutellum marked with yellow maculae and irregular patches; forewing with a distinct hyaline transverse band medially. Crown broadly rounded and distinctly protruding anteriorly, median length approximately 1.5 times as long as distance between eyes. Ocelli separated from adjacent eyes by about three times their own diameter. Antennae located just above midline of eyes. Frontoclypeus narrow at base, gradually widening toward apex.

***Male genitalia*.** Pygofer side subquadrangular, sparsely covered with short setae; posteroventral process elongate and strongly curved dorsad, with short dorsal spine near base. Valve semicircular. Subgenital plate with digitate apical extension relatively long and slender. Style elongate, markedly narrowed apically. Aedeagal shaft lanceolate in dorsal or ventral view; shaft with a pair of lamellate processes on both dorsal and ventral surfaces at mid-length; gonopore ventral, subapical; dorsal apodeme well developed. Connective stem slightly longer than arms.

Distribution. China (Fujian: Guobao, Huboliao).

Etymology. The new species name is derived from the Latin word *digitulatus* (finger-like), referring to the apical portion of the subgenital plate, which is abruptly constricted into a finger-like process.

Remarks. The new species is externally indistinguishable from *D. ineffectus*, but the male genitalia differ as follows: aedeagal shaft in ventral view gradually widened from the base to middle and then tapered evenly toward apex (continuously narrowed from base to tip in *D. ineffectus*); in lateral view, shaft distinctly swollen on both dorsal and ventral sides, with smooth margins (swelling restricted to ventral side only in *D. ineffectus*; dorsal margin finely serrate); pygofer side with slender dorsal spine near base of posteroventral process (spine absent in *D. ineffectus*). The new species also resembles *D. henanensis* in overall appearance but differs in several key aspects: crown more strongly produced anteriorly (less angulate in *D. henanensis*); subgenital plate abruptly constricted subapically into a distinct finger-like process (apex simply rounded in *D. henanensis*); ventral process of pygofer more elongate and slender; style more tapered apically; aedeagal shaft slightly inflated ventrally at mid-length in lateral view (evenly tapered in lateral view in *D. henanensis*).

***Drabescus guangdongensis* Qu, Li, Dietrich & Dai, sp. nov.**

https://zoobank.org/D47EBCAD-79CD-4534-B2FC-2D10327775AF

Fig. 5

Material examined. • ***Holotype***, ♂ (GUGC), CHINA: Guangdong Province, Chebaling National Nature Reserve, 10.V.2013, collected by Meng Jiao and Bin Li.

Description. Length (including tegmen): 11.8 mm.

Body yellowish brown, pronotum and scutellum with numerous yellow maculae or patches. Forewing with a distinct hyaline transverse band near midlength. Face and frontoclypeus yellowish brown, bearing short, dark-brown bands; antennal pits and eyes light brown to brown, remaining areas bright yellow. Crown anterior margin broadly rounded, no longer medially than next to eyes in dorsal view. Ocelli each separated from adjacent eye by approximately three times its own diameter. Antennae situated anterodorsally to eyes. Face wider than long. Frontoclypeus gradually widened from base to apex.

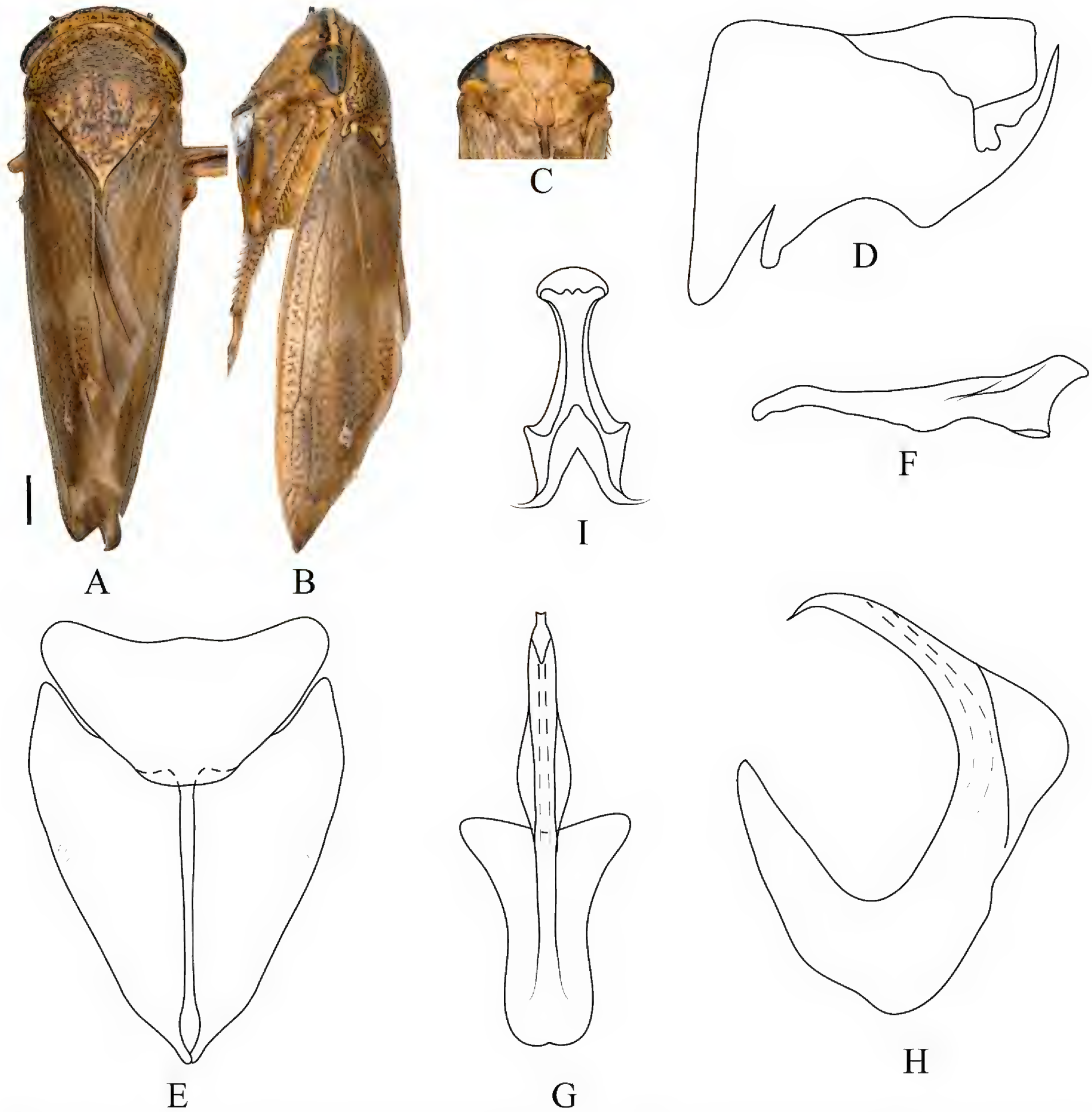

Figure 5. *Drabescus guangdongensis* Qu, Li, Dietrich & Dai, sp. nov. **A.** Male habitus, dorsal view; **B.** Same, lateral view; **C.** Face; **D.** Pygofer, lateral view; **E.** Valve and subgenital plate, ventral view; **F.** Style, dorsal view; **G.** Aedeagus, ventral view; **H.** Same, lateral view; **I.** Connective, ventral view. Scale bars: 1.0 mm (**A–C**).

***Male genitalia*.** Pygofer side distinctly angulate posteroventrally, posteroventral process relatively short, with toothlike dorsal spine near base. Valve subquadrate, nearly semicircular. Subgenital plate apex narrowed into short, finger-like process. Style slender and sinuate, with apex smoothly rounded. Aedeagal shaft cylindrical, slightly inflated at midlength in ventral view; shaft curved dorsally with conspicuous, median, posterior swelling in lateral view. Gonopore ventral, subapical. Connective stem distinctly longer than arms.

Distribution. China (Guangdong: Chebaling).

Etymology. The new species name is derived from the province where the type locality is located, Guangdong.

Remarks. Although the new species closely resembles *D. ineffectus* in overall appearance, the male genitalia differ as follows: aedeagal shaft in ventral view slender with slight lateral swellings near midlength (evenly tapered from base to apex in *D. ineffectus*); shaft in lateral view smooth-edged, with a median posterior swelling and greatest width nearly twice the maximum ventral width (denticulate dorsal margin and less pronounced median swelling in *D. ineffectus*, greatest lateral width distinctly less than twice ventral width). The new species also closely resembles *D. multipunctatus* in external morphology but can be distinguished by the following characters of the male genitalia: the aedeagal shaft in ventral view slightly inflated at mid-length (not inflated medially in *D. multipunctatus*); aedeagal shaft in lateral view more strongly curved dorsally, moderately swollen at middle, and with smooth margins (less strongly curved dorsally, not swollen medially, and with serrate margins in *D. multipunctatus*). Furthermore, the arms of the connective are shorter than the stem (subequal to stem in *D. multipunctatus*).

***Drabescus millesimus* Li, Qu & Dai, sp. nov.**

https://zoobank.org/148B2EAE-5AE4-4AE3-AB2E-372FE99A56AE

Fig. 6

Material examined. • ***Holotype***, ♂ (GUGC), CHINA: Guangxi Province, Huaping National Nature Reserve, 19.V.2012, collected by Hu Li. • ***Paratypes***, 2♂♂ (GUGC), same locality as holotype, 19.V.2012 collected by Zhihua Fan.

Description. Length (including tegmen): 11.5–12.1 mm.

Body yellowish brown; pronotum and scutellum densely covered with yellow spots or irregular patches; face uniformly yellowish brown. Head with crown anterior margin broadly rounded and slightly protruding. Ocelli separated from adjacent eyes by about twice their own diameter. Antennae situated anterodorsally to upper angles of eyes. Face wider than long.

***Male genitalia*.** Pygofer side broad basally and narrowed apically, covered with microsetae; posteroventral process slender and strongly curved dorsad, with small dorsal spine at base. Valve subrectangular. Subgenital plate with finger-like distal extension relatively short. Style slender, margins weakly undulate. Aedeagal shaft dorsoventrally flattened, in ventral view with sinuate margins, moderately inflated medially, gradually tapered subapically; ventral surface with a few subtriangular denticles and numerous longitudinal ridges; shaft in lateral view dorsally curved, tapering continuously from base to apex, apex recurved in lateral view. Gonopore subapical on ventral surface. Connective stem tapered posteriorly, much longer than arms.

Distribution. China (Guangxi: Huaping).

Etymology. The species name is derived from the Latin word *millesimus* (thousandth), referring to the 1000th new species described by Professor Li Zizhong.

Remarks. The new species is virtually indistinguishable from *D. ineffectus* in external appearance, but the male genitalia differ as follows: aedeagal shaft in ventral view gradually expanded from base to middle then tapered evenly toward apex (continuously narrowed from base to apex in *D. ineffectus*); shaft in lateral view narrowed evenly from base to apex and with finely serrate ventral margin (distinctly swollen at mid-length with a serrate dorsal margin in *D. ineffectus*).

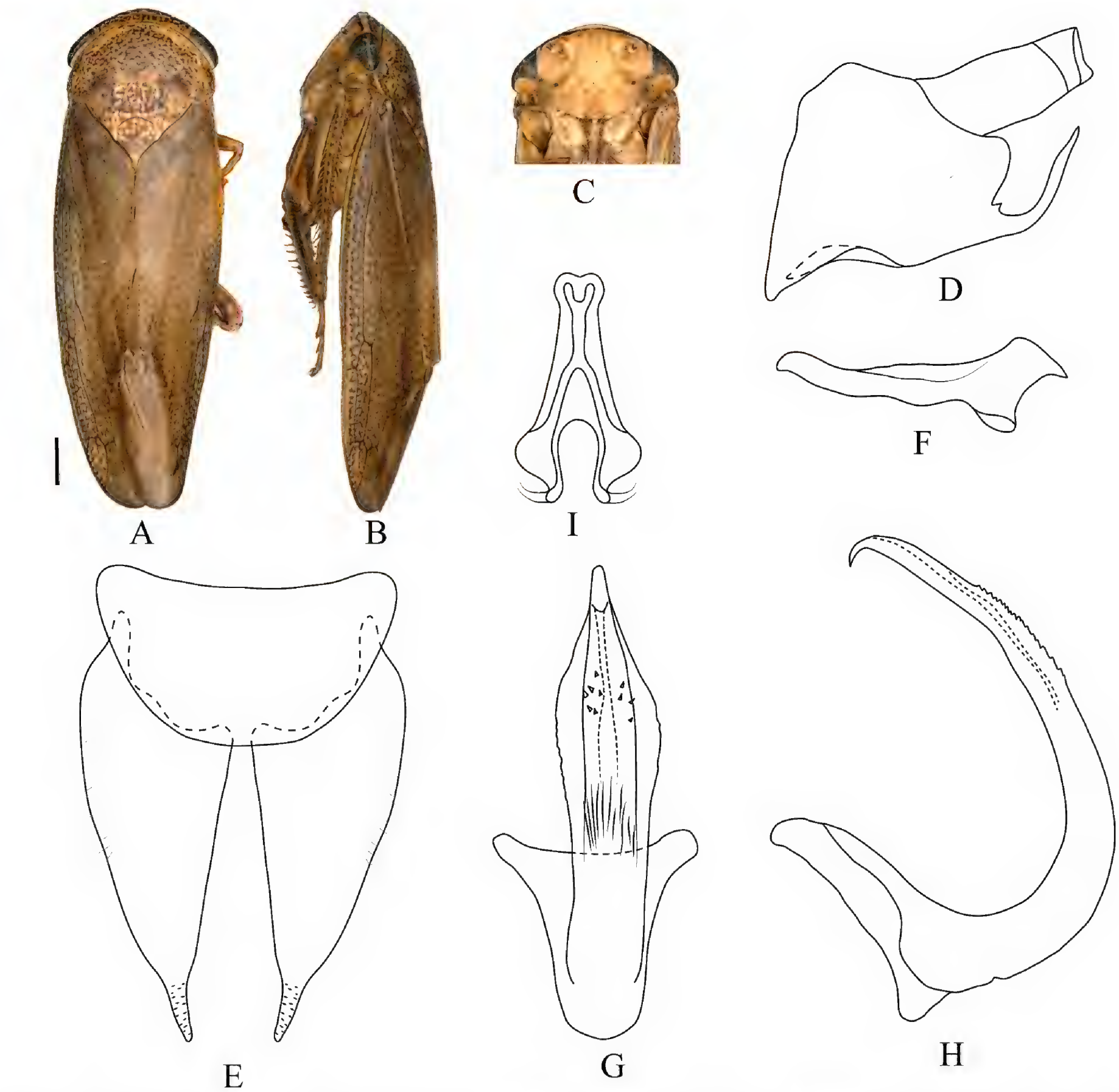

Figure 6. *Drabescus millesimus* Li, Qu & Dai, sp. nov. **A.** Male habitus, dorsal view; **B.** Same, lateral view; **C.** Face; **D.** Pygofer, lateral view; **E.** Valve and subgenital plate, ventral view; **F.** Style, dorsal view; **G.** Aedeagus ventral view; **H.** Same, lateral view; **I.** Connective, ventral view. Scale bars: 1.0 mm (**A–C**).

Furthermore, the inner margin of the pygofer process is smooth with a single small basal spine in the new species (distinctly crenulate in *D. ineffectus*).

Drabescus trigonius **Qu, Li, Dietrich & Dai, sp. nov.**

https://zoobank.org/93A2F2A9-2ABB-4A37-821E-B7ED6501D0F1

Fig. 7

Material examined. • ***Holotype***, ♂ (GUGC), CHINA: Guangxi Zhuang Autonomous Region, Damingshan National Nature Reserve, 4.V.2012, collected by Zhihua Fan.

Description. Length (including tegmen): 11.4 mm.

Body yellowish brown, densely covered with minute black spots or patches. Face yellow; ocelli bright yellow; eyes dark brown. Crown anterior margin with a distinct

carina containing multiple fine, transverse striations; crown strongly and evenly rounded, median length 1.5 times the distance between eyes. Ocelli each situated 2–3 times their own diameter from adjacent eye. Face including eyes distinctly wider than long. Antennae nearly parallel with dorsal angle of eyes. Frontoclypeus slightly apically inflated; lateral frontal sutures extending to corresponding ocelli. Transverse suture between anteclypeus and frontoclypeus faint; frontoclypeal sulcus distinct.

Male genitalia. Pygofer side with few small setae near apical margin, posteroventral processes with short, rounded dorsal projection near base. Valve semicircular. Subgenital plate subtriangular, margins with minute setae. Style apex relatively stout, curved slightly mesad. Aedeagus shaft laminar, margins undulate and dorsoventrally flattened in ventral view; subapical region abruptly constricted into a cylindrical extension toward apex; shaft bowed dorsad, subapically inflated with

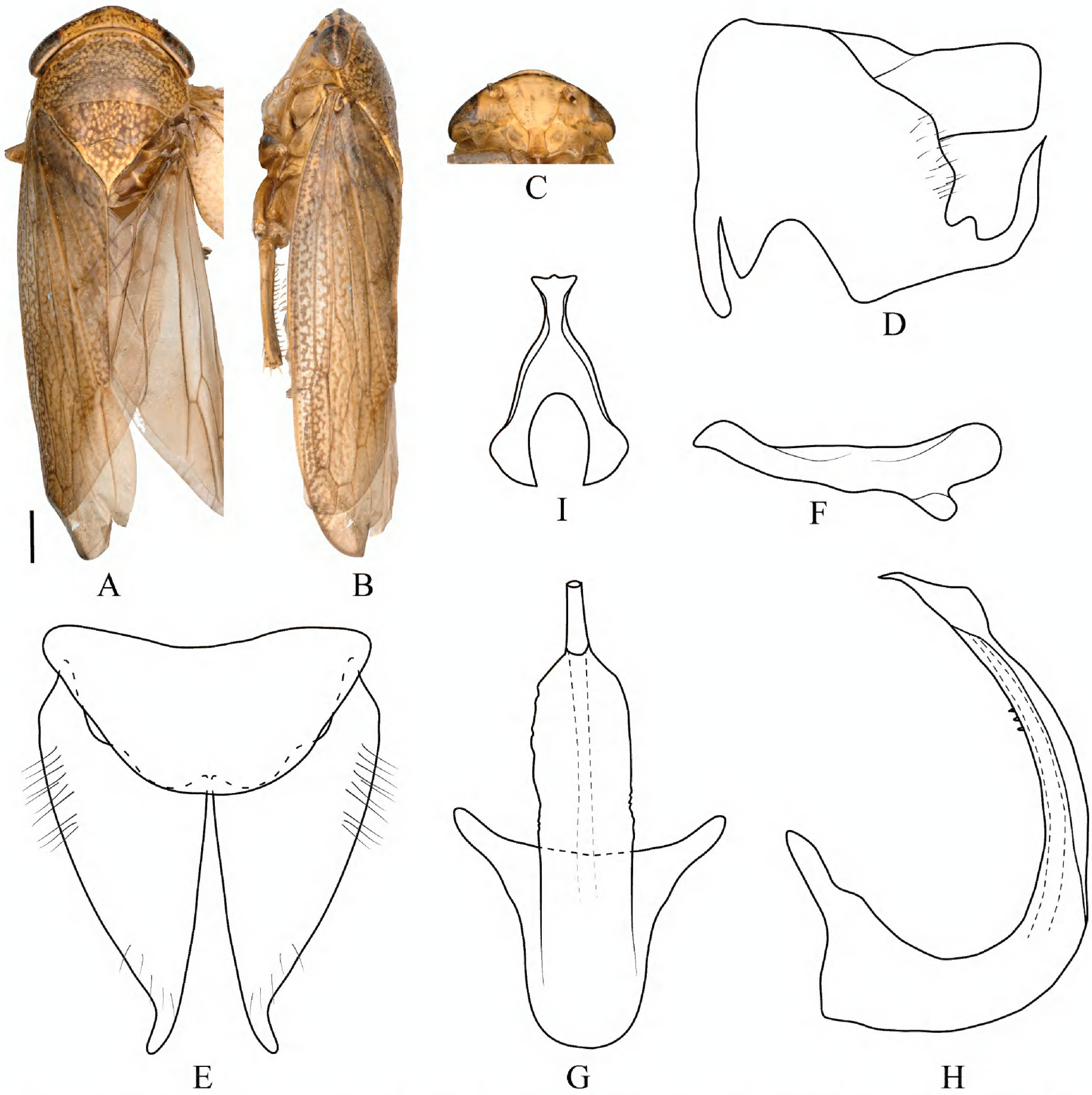

Figure 7. *Drabescus trigonius* Qu, Li, Dietrich & Dai, sp. nov. **A.** Male habitus, dorsal view; **B.** Same, lateral view; **C.** Face; **D.** Pygofer, lateral view; **E.** Valve and subgenital plate, ventral view; **F.** Style, dorsal view; **G.** Aedeagus ventral view; **H.** Aedeagus, lateral view; **I.** Connective, ventral view. Scale bars: 1.0 mm (**A–C**).

three small, triangular processes on ventral surface in lateral view; gonopore ventral, subapical. Connective with stem much shorter than arms.

Distribution. China (Guangxi: Damingshan).

Etymology. The species name is derived from the Latin word *trigonius* (triangular), referring to the ventral surface of the shaft bearing three small, triangular processes.

Remarks. The new species closely resembles *D. ineffectus* in general habitus, but the male genitalia readily separate them as follows: aedeagal shaft in ventral view abruptly constricted subapically and continued as a slender, columnar extension (shaft evenly tapered from base to apex in *D. ineffectus*); shaft in lateral view, conspicuously inflated subapically, dorsal margin with three small, triangular processes (shaft swollen medially with a serrated dorsal margin in *D. ineffectus*). Additionally, the inner margin of the process on the pygofer side is smooth in the new species (distinctly crenulate in *D. ineffectus*).

Discussion

We establish the *Drabescus ineffectus* species group based on a suite of shared morphological characters in external features and male genitalia. Although these species are highly similar in general appearance, they can be unambiguously distinguished by diagnostic differences in genital structures, supporting their recognition as distinct species. The observed distribution, with most members of the group recorded from southern China, may indicate a pattern of micro-allopatric speciation, likely facilitated by geographic isolation within mountainous habitats.

While the monophyly of the *D. ineffectus* group is well supported by morphological evidence, future phylogenetic studies incorporating molecular data are essential to test its validity and elucidate evolutionary relationships among the included species. This study reaffirms the critical value of male genital morphology for species delimitation within *Drabescus* and underscores the persistent need for taxonomic revision in diverse but understudied insect groups.

All five new species described here are diagnosed and described based exclusively on male specimens. Despite extensive sampling efforts at the respective type localities using both sweep nets and light traps, no females reliably assignable to these species were found. Although a small number of female specimens were collected from the same sites, none could be confidently assigned to any of the new species. Consistent with patterns in most other deltocephaline leafhoppers (Zhang and Webb 1996; Viraktamath et al. 2022), species delimitation and identification in *Drabescus* rely almost entirely on characters of the male genitalia, while females of most species lack unambiguous, species-specific diagnostic traits. The male genitalic characters documented for each new species in the present study are highly discrete and provide unambiguous, stable criteria for species recognition. Targeted future sampling at the type localities, particularly efforts to collect mating pairs, will likely facilitate the discovery and formal association of conspecific females.

Acknowledgements

We are grateful to Bin Li, Jiankun Long, Zhihua Fan, and Meng Jiao (Institute of Entomology, Guizhou University, Guiyang, China) for their kind offering the materials for study.

References

Anufriev GA, Emeljanov AF (1988) Suborder Cicadinea (Auchenorrhyncha). Nauka, Leningrad, 496 pp.

Cai P, He JH (1998) Five new species of subfamily Iassinae from Mt. Funiu in Henan (Homoptera: Cicadellidae). China Agricultural Science and Technology Press, Beijing, 368 pp.

Cai P, Shen XC (1999) Nine new species of Cicadellidae from Baotianman Nature Reserve (Homoptera: Cicadellidae). China Agricultural Science and Technology Press, Beijing, 405 pp.

Cai P, Jiang JF (2002) A new species of *Drabescus* Stål from Henan Province, China (Homoptera: Cicadelloidea: Selenocephalinae). China Agricultural Science and Technology Press, Beijing, 453 pp.

Distant WL (1908a) Descriptions of some Rhynchota from Ruwenzori. Annals and Magazine of Natural History (Series 8) 2: 436–444. https://doi.org/10.1080/00222930808692506

Distant WL (1908b) Rhynchota. IV. Homoptera and appendix (Pt.). The Fauna of British India, including Ceylon and Burma. Taylor and Francis, London, [xv +] 501 pp.

Kato M (1933) Notes on Japanese Homoptera, with descriptions of one new genus and some new species. Entomological World Tokyo 1: 452–471.

Kuoh CL (1966) The Economic Insect Fauna of China. Vol. 10. Homoptera: Cicadellidae. Science Press, Beijing, 307 pp.

Kuoh CL (1985) New species of *Drabescus* and a new allied genus (Homoptera: Iassidae). Acta Zoologica Sinica 31(4): 377–383.

Li ZZ, Wang LM (2005) Cicadellidae: Hecalinae, Coediinae, Iassinae, Typhlocybinae Euscelinae, Nirvaninae and Evacanthinae. Guizhou Science and Technology Press, Guiyang, 462 pp.

Lu L, Webb MD, Zhang YL (2019) A new species of the leafhopper genus *Drabescus* Stål (Hemiptera: Cicadellidae: Deltocephalinae) from China, with a checklist and key to species. Zootaxa 4612(2): 237–246. https://doi.org/10.11646/zootaxa.4612.2.6

Matsumura S (1912) Die Acocephalinen und Bythoscopinen Japans. The Journal of the College of Agriculture, Tohoku Imperial University, Sapporo, Japan 4(7): 279–325.

Melichar L (1903) Homopteren-Fauna von Ceylon. Felix L. Dames, Berlin, [iv +] 248 pp.

Rao KR (1989) Descriptions of some new leafhoppers (Homoptera: Cicadellidae) with notes on some synonymies and imperfectly known species from India. Hexapoda (Insecta Indica) 1(1–2): 59–84.

Schumacher F (1915) Der gegenwärtige Stand unserer Kenntnis von der Homopteren-Fauna der Insel Formosa unter besonderer Berücksichtigung von Sauter'schem Material. Mitteilungen aus dem Zoologischen Museum in Berlin 8: 73–134.

Shang SQ, Webb MD, Zhang YL (2014) Key to Chinese species of the leafhopper genus *Drabescus* (Hemiptera: Cicadellidae: Deltocephalinae) with description of a new species. Zootaxa 3852(1): 141–146. https://doi.org/10.11646/zootaxa.3852.1.7

Shang SQ, Zhang YL (2007) Four species of the leafhopper subfamily Selenocephalinae (Hemiptera: Cicadellidae) as new records from China. Sciencepaper Online 2(6): 430–433.

Signoret V (1880) Essai sur les Jassides Stål, Fieb. et plus particulierement sur les Acocéphalides Puton. Annales de la Société Entomologique de France, Paris 10(5): 189–212.

Stål C (1858) Hemipterologiska bidrag. Öfversigt af Kongliga Svenska Vetenskaps-Akademiens Förhandlingar. Stockholm 15: 433–454.

Stål C (1870) Hemiptera insularum Philippinarum–Bidrag till Philippinska öarnes Hemipter-fauna. Öfversigt af Kongliga Svenska Vetenskaps-Akademiens Förhandlingar, Stockholm 27: 607–776 [pls 7–9]. https://doi.org/10.5962/bhl.title.61898

Viraktamath CA, Webb MD, Yeshwanth HM (2022) Review of the leafhopper genus *Drabescus* Stål (Hemiptera: Cicadellidae: Deltocephalinae) in the Indian subcontinent with description of one new species. Zootaxa 5128(2): 225–247. https://doi.org/10.11646/zootaxa.5128.2.4

Walker F (1851) List of the Specimens of Homopterous Insects in the Collection of the British Museum. Part III. Order of the Trustees, British Museum, London, 271 pp.

Walker F (1858) List of the Specimens of Homopterous Insects in the Collection of the British Museum. Supplement. Order of Trustees, British Museum, London, 307 pp. https://doi.org/10.5962/bhl.title.34441

Wang JJ, Qu L, Xing JC, Dai RH (2016) Three new species of the leafhopper genus *Drabescus* Stål (Hemiptera: Cicadellidae: Deltocephalinae) from China. Zootaxa 4132(1): 118–126. https://doi.org/10.11646/zootaxa.4132.1.10

Xu D, Zhang Y (2023) Taxonomy of the leafhopper genus *Drabescus* Stål (Hemiptera: Cicadellidae: Deltocephalinae) with description of two new species from China. Zootaxa 5264(3): 393–404. https://10.11646/zootaxa.5264.3.7

Yang JK, Zhang LS (1995) Homoptera: Cicadelloidea. Zhejiang Science and Technology Press, Hangzhou, 539 pp.

Yu Z, Webb MD, Dai RH, Yang MF (2019) Three new species in the leafhopper tribe Drabescini (Hemiptera, Cicadellidae, Deltocephalinae) from southern China. ZooKeys 846: 43–53. https://doi.org/10.3897/zookeys.846.34003

Zhang YL, Shang SQ (2003) Three new species of the leafhopper genus *Drabescus* Stål (Homoptera: Cicadellidae: Selenocephalinae) from China. Entomotaxonomia 25(2): 95–101.

Zhang YL, Webb MD (1996) A revised classification of the Asian and Pacific selenocephaline leafhoppers (Homoptera: Cicadellidae). Bulletin of the Natural History Museum Entomology Series 65(1): 1–103.

Zhang YL, Zhang WZ, Chen B (1997) Selenocephaline leafhoppers (Homoptera: Cicadellidae) from Mt. Funiushan in Henan Province. Entomotaxonomia 19(4): 235–245.

Additional

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Artificial Intelligence (AI) use

The authors accept full responsibility for the content of the manuscript, including the disclosure of any use of AI.
No AI tools were used in the preparation of this manuscript.

Funding

The study was supported by the National Natural Science Foundation of China (grant no. 32160119), the Program of Excellent Innovation Talents, Guizhou Province, China (grant no. 20206003-2) and the Foshan Self-funded Science and Technology Innovation Project (grant no. 2520001002836).

Author contributions

Conceptualization: HL, ZL, LQ. Formal analysis: CHD, ZL. Funding acquisition: LQ, RD. Investigation: WJ, HL, LQ. Methodology: RD, ZL. Project administration: RD. Supervision: CHD, ZL. Writing - original draft: LQ. Writing - review and editing: HL, CHD.

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Data availability

All of the data that support the findings of this study are available in the main text.